THE PHYLOGENY OF THE NEMOCERA, WITH NOTES ON THE LEG BRISTLES, HAIRS AND CERTAIN MOUTH GLANDS OF DIPTERA.[1]

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Professor Williston has published a paper[2] on the antennæ of Diptera which is not only a remarkable analysis of these organs, but one showing an encyclopædic knowledge. His deductions combined with his observations on other characters seem to me of great weight and importance, and may lead to a more exact classification of the order.

On page 326 of the cited paper, in commenting on the number of antennal joints in the different families of Diptera, he says: "We are at once struck with the predominance of five groups having a maximum normal number of sixteen, fifteen, ten, six and five. And I venture to suggest that these five groups represent in the main five different divergent phyla of Diptera." These groups are:

Group 1.—Families having from twelve to sixteen joints: Tipulidæ, Cecidomyidæ, Psychodidæ, Mycetophilidæ, Pachyneurinæ, Rhyphidæ.

Group 2.—Families with from six to fifteen joints: Dixidæ, Culicidæ, Blepharoceridæ, Chironomidæ.

Group 3.—Families with from seven to ten joints: Scatopsinæ, Simulidæ, Xylophaginæ, Stratiomyidæ, Acanthomeridæ, Tabanidæ.

Group 4.—Families with from three to six joints: Nemistrinidæ, Lonchopteridæ, Phoridæ, Cyclorrhapha.

[1] The MS. of the present article was sent to me some time before his death by the late Mr. Weschè, with a request for comment and criticisms. In editing the paper, which Mr. Weschè had not quite completed, I have made no changes whatever except verbal ones, and have omitted only a few immaterial parts. Most of his conclusions seem well taken, and it is to be regretted that the author could not have been spared to continue his researches along the fruitful lines that he had begun.—S. W. WILLISTON.

[2] BIOLOGICAL BULLETIN, XIII., p. 324, 1907.

Group 5.—Families with from three to five joints: Mydaidæ, Apioceridæ, Asilidæ, Therevidæ, Bombylidæ, Dolichopodidæ, Empidæ.

The Orphnephilidæ (11, 12), Bibionidæ (8–12), Leptinæ (3–8) and Scenopinidæ (3) fill in gaps between the chief groups. But it is obvious that the author was not dogmatic in the formulation of these groups, as later it is stated (p. 330) that "the antennæ, taken separately, are only partial evidences of relationship. They must be correlated with all other organs of the body, and must harmonize with theories based upon other organs." Carrying out this idea, and quite agreeing that no single character can be relied upon, I have endeavored to test the validity of these phyla by other structures, for the most part microscopic, such as the eyes, the trophi, and the genitalia; and I have embodied the results of my studies in a series of tables.

These tables have been made to show the dominant characters of the families; every large family has numerous exceptions and specializations, as, for instance, the labium in the Dolichopodidæ is nearly always short, though we know that it is long in *Orthochile*, and longer than normal in *Gymnopterus*. In speaking of dominant characters I must guard myself by saying that my cabinet of dissections is composed mostly of the commonest and most widely distributed forms, selected where the material for dissection was most abundant; there is, hence, probably a margin of error.

The tabulated observations are mostly contained in four papers previously published by myself: "The Mouthparts of the Nemocera," 1904, with additions and corrections (1909), (*Journal of the Royal Microscopical Society*); "The Genitalia of the Sexes in Diptera" (*Trans. Linn. Soc.*, London, 1906), and "The Structure of the Surface and the Sexual Characters of the Eyes of Diptera" (*Journal Queckett Club*, 1909). Many additional facts since observed have been incorporated in the tables.

The following explanations will be necessary for a full comprehension of these tables. The trophi are fully analyzed. Their most important parts, from the point of view of phylogeny, seem to be the tracheæ of the paraglossæ, the mentum, the palpi, and the pharyngeal pump. The tables of the genitalia give the

characters of the interior and more invisible parts, which I have formulated in a previous paper.[1] They will be described as of certain types:

Type 1.—A long flagelliform tube, as in *Tipula*, or an approximation to that type.

Type 2.—A prominent chitinous bulb, with lateral processes, as in *Ptychoptera*.

Type 3.—A low membranous process supported by chitinous levers, as in *Gymnoplista* and *Culex*.

In the second case the nature of the ancillary claspers are given (*a*) as simple hooks, as in many Muscidæ, (*b*) jointed, as in the Tabanidæ, (*c*) or a simple unsegmented cercus-like appearance, as in the Bibionidæ. Three types of ovipositor are differentiated:

Type 1.—Telescopic or protrusile, as in *Calliphora* or *Dolichopus*.

Type 2.—Nontelescopic, as in *Tipula*, where it can scarcely be said to exist.

Type 3.—Short segmented, such as is found in the Empidæ.

Further the appendages of the egg-guide are tabluated, as (*a*) cercus-like, as in *Bibio* or *Musca;* (*b*) uncinate, as in *Tipula* or many Muscidæ; (*c*) styliform, as in *Psychoda* or *Pipunculus*, where it is probably a fusion of the pair of forceps.

The number of receptacula is noted. The types of penis and ovipositor seem to me the more important characters. Among the characters of the eyes, holopticism, dichopticism, and the greater width of the female front are given; and the absence or presence of ocelli is also noted.

It may be stated that in certain families the compound eyes are chitinous plates pierced by circular facets or lenses; this opaque structure is much reduced in other families till only strips of chitin separate the hexagonal facets. Finally in specialized groups all traces of opaque structure are lost.

These tables may be examined in two ways. The most important characters may be noted and the tables consulted to see how far they are in agreement; or the characters of the group may be added up and averaged. The latter method shows that

[1] "Notes on the Value of the Genitalia in Phylogeny." *Trans. Entom. Soc. London*, 1908.

TABLE I.

MOUTH CHARACTERS OF THE NEMOCERA.

	Group.	Labium.				Tracheæ.		Mentum.				Labrum.				Hypopharynx.			Palpi.				Sense Organs.			Mandibles.				Maxillæ.		Pharyngeal Pump.			
	Williston's Phyla.	Short.	Long.	Membranous.	Chitinous.	Present.	Absent.	Undeveloped.	Developed.	Extremely Developed.	Median Suture.	Strong.	Weak.	Ciliated.	Vestigial.	Ciliated.	Weak.	Vestigial.	Maxillary.	Labial.	4 Joints.	2 Joints.	1 Joint.	Absent.	Present.	Peculiar.	Fully Developed.	Vestigial.	In Ventral Side of Labium.	Fused into Dorsal Side of Labium.	Laciniæ Present.	Stipites and Cardines Present.	Vestigial.	3 Plates.	2 Plates.	Vestigial.	Absent.
Cecidomyidæ	I	*		*			*	*				*	*			*			*		*			*				*			*	*					
Mycetophilidæ	I	*		*			*	*				*	*			*			*		*			*				*			*	*					
Bibionidæ — *Bibio*	O	*		*			*	*				*	*			*			*		*			*				*			*	*					
Bibionidæ — *Dilophus*	O		*				*	*					*				*			*					*											
Bibionidæ — *Scatopse*	3	*		*			*	*				*		*		*				*			*									*					
Simulidæ	3	*		*			*	*		?		*	*			*			*		*			*				*			*	*					
Chironomidæ	2	*		*			?	*		?		*	*			*			*		*			*				*			*	*					
Ceratopogon	2		*				*					*	*			*			*		*			*				*			*	*					
Psychodidæ	I	*		*			*	*				*	*			*			*		*			*				*			*	*					
Culicidæ — *Corethra*	2	*		*			*	*			?	*	*			*			*		*			*				*			*	*					
Culicidæ — *Mochlonyx*	2	*		*		?	*	*			?	*	*			*			*		?	?		*			♂	*			*	*					
Culicidæ — *Culex*	2		*				*	*		*		*	*			?			*		?			*				*			*	*					
Ptychoptera	I	*		*		*		?				*	*			*	*		*		*			*				*			*	*					
Tipulidæ	I	*		*			*	*				*	*			*		*	*		*			*				*			*	*					
Rhyphidæ	I	*		*			*	*			*	*	*			*[5]			*		*			*				*			*	*					

[1] Only a remnant of the fused parts.

[2] In one species.

[3] Fused together and in the same condition as the other Tipulidæ.

[4] This clearly shows as three in one preparation. I am not certain of two.

[5] Very vestigial cilia.

TABLE II.

CHARACTERS OF MOUTH IN BRACHYCERA AND CYCLORRAPHA.

	Group.	Labium.				Tracheæ.		Mentum.				Labrum.				Hypopharynx.					Palpi.				Sense Organs.			Mandibles.				Maxillæ.			Pharyngeal Pump.			
	Williston's Phyla.	Short.	Long.	Membranous.	Chitinous.	Present.	Absent.	Undeveloped.	Developed.	Extremely Developed.	Median Suture.	Strong.	Weak.	Ciliated.	Vestigial.	Ciliated.	Weak Unciliated.	Strong Unciliated.	Vestigial.	Maxillary.	Labial.	4 Joints.	2 Joints.	1 Joint.	Absent.	Present.	Peculiar.	Fully Developed.	Vestigial.	In Ventral Side of Labium.	Fused into Dorsal Side of Labium.	Laciniæ Present.	Stipites and Cardines Present.	Vestigial.	3 Plates.	2 Plates.	Vestigial.	Absent.
Asilidæ	5	*			*		*					*				*				*				*	*			*				*	*					
Empidæ	5		*	*	*[1]	*	1		*		*	*					*	*		*			*	*	*						*	*			*		
Dolichopodidæ	5	*		*		*[2]			*		*	*		*				*		*	*			*								*			*		
Phoridæ	4	*		*		*			*		*	*	*					*		*		*[3]	*	*[4]	*					*		*[5]	*				*
Lonchopteridæ	4	*		*		*			*		*	*						*		*			*	*						*		*					*
Leptidæ	o	*		*		*		*[6]	*		*	*				*		*		*			*	*						*		*					*
Stratiomyidæ	3	*		*		*			*		*	*		*			*	*		*		*		*		*				*		*					*
Tabandidæ	3		*	*		*		*	*[7]		*	*						*		*		*		*		*[9]	*	♂		*		*					
Bombylidæ	5		*	*		*			*		*	*						*		*			*		*[10]				*		*					?
Cyrtidæ	o		*[11]		*				*	*										*			*														
Platypezidæ	4	*		*		*			*		*		*				*			*			*	*					*		*	*[12]					*
Pipunculidæ	4	*		*		*			*		*		*				*			*	*?		*		*				*	*?		*					*
Syrphidæ	4		*	*		*			*				*				*			*			*	*						*	*	*					*
Conopidæ	4		*		*	*			*	*										*			*														*
Muscidæ	4	*	*	*	*	*	*		*	*		*	*		*			*	*		*			*	*						*	*[13]	*					*

[1] In *Hybos*.
[2] Peculiar.
[3] In several species.
[4] Only in *Trineura*.
[5] In an atrophied condition in a few species.
[6] In *Leptis*.
[7] In *Hæmatopota* and other species of *Tabanus*.
[8] In *T. africanus* and *H. pluvialis*.
[9] In *Pangonia longirostris*.
[10] Small in *Comptosia occellata* New.
[11] Or aborted.
[12] Vestigial in several species.
[13] In some Acalyptrates.

the points of agreement are fairly strong in group 1, strong also in group 2, weak in groups 3 and 4, and fairly strong in group 5.

If the weak groups are examined anomalies will be seen in group 3; the Simulidæ seem out of place. I have lately found a structure in the palpi of *S. reptans* and *Rhyphus fenestralis* and *R. punctatus* ♀, which convince me of a near relationship and common ancestry of these two families. By adding *Simulium* to group 1 there results a larger proportion of similar characters.

TABLE III.

CHARACTERS OF THE GENITALIA IN THE NEMOCERA.

	Group.	Male.						Female.								
		Type of Penis.			Claspers Forcipes.			Ovipositor.			Appendages.			Receptacula.		
	Williston's Phyla.	Type 1.	Type 2.	Type 3.	Cercilike.	Simple Hamate.	Jointed Hamate.	Non-telescopic.	Short Telescopic.	Telescopic.	Cercilike.	Uncinate.	Styliform.	One.	Two.	Three.
Cecydomyidæ	1	*				*		*			*			*[1]		
Mycetophilidæ	1	*			*	*			*		*					
Bibionidæ	0	*			*			*			*					*
Scatopse	3	*				*		*			*			*		
Simulidæ	3	*			*			*			*			*		
Chironomidæ	2	*[2]				*		*			*				*[3]	
Psychodidæ	1	*				*		*					*			
Culicidæ	2		*			*		*				*				*
Ptychopteridæ	1			*		*		*				*				*
Erioptera	1							*				*				*
Tipulidæ	1	*				*		*				*				*
Rhyphidæ	1	*[4]			*			*			*			*		

[1] Where nothing is stated these organs are not chitinous and do not show in preparations.

[2] Approximates to that of the Rhyphidæ.

[3] 1–2 in *Ceratopogon*.

[4] Complicated and peculiar, but approximates.

Nor can I reconcile myself to the inclusion of the Scatopsinæ, though this subfamily, unlike the Simulidæ, will not fit well into group 1, notwithstanding that the genitalia show marked affinities with those of *Tipula*. The very marked specialization of the mouth structure and the three ocelli outweigh in importance the archaic eye structure, the bristle structure, especially that of the legs, and pharyngeal pump; I can not at present suggest

any change in the position they now occupy among the Bibionidæ, though I consider this family the most specialized of the Nemocera.

TABLE IV.

CHARACTERS OF THE GENITALIA IN THE BRACHYCERA AND CYCLORRAPHA.

	Group.	Male.						Female.								
		Type of Penis.			Claspers.			Ovipositor.			Appendages.			Receptacula.		
	Williston's Phyla.	Type 1.	Type 2.	Type 3.	Cercilike.	Simple Hamate.	Jointed Hamate.	Non-telescopic.	Short Telescopic.	Telscopic.	Cercilike.	Uncinate.	Styliform.	One.	Two.	Three or More.
Asilidæ	5	*				*		*			*	*			*	
Empidæ	5	*				*			*		*			*		
Dolichopodidæ	5	*				*				*		*		*[1]		
Phoridæ	4		*	*	*					*	*			*[1]		
Lonchopteridæ	4		?[2]	?	*			*			*				*[3]	
Leptidæ	0	*					*		*		*					*
Stratiomyidæ	3	*			*				*		*					*
Tabanidæ	3	*[4]					*	*			*					*
Bombylidæ	5	*			*			*			*					*
Cyrtidæ	0	*			*			*			*			?		
Platypezidæ	4	*			*	*			*		*				?	
Pipunculidæ	4	*				*		*					*			*
Syrphidæ	4			*	*	*		*		*	*	*				*
Conopidæ	4			*	*			*	*		*	*				*
Muscidæ	4			*		*		*	*	*	*	*	*	*	*	*

[1] Invisible in preparations.

[2] Indefinite, suggests affinities with *Dolichopus*.

[3] Transparent, only demonstratable by dissection.

[4] And theLeptidæ are nearer type 1 than 2 or 3. They only approximate.

If any reliance is to be placed on the genitalia, the Stratiomyidæ must belong in group 3, since the male type clearly connects the family with the Asilidæ, Empidæ and Dolichopodidæ. And the condition of the mentum sustains this view, though character of the leg pubescence is less decisive. The genitalia and venation of the Tabanidæ are so close that it seems impossible to separate the family; both find their place in group 5.

These points seem to show that group 3 is an artificial one; nor does group 4 inspire me with confidence, since I can not separate the Phoridæ and the Lonchopteridæ from the Asilidæ, Empididæ and Dolichopodidæ. Group 4 must be narrowed down to the Cyclorrhapha, and even here I think that I can trace the pedigree to group 5, if not to group 1.

I have now completed my analysis of the groups suggested by Williston from the antennal characters, so far as my imperfect data will permit, and I think that it shows that they furnish important hints as regards the phylogeny, particularly of the older flies, though the light they throw is intermittent and flickering. From their exposed position and frail structure the antennæ are subject, in the swiftest flying insects, to more than the usual risk of injury, which is possibly one reason for the extreme variation they show, ranging from three joints in the Scenopinidæ to thirty-nine in *Cerozodia*.

TABLE V.

STRUCTURE OF EYES IN NEMOCERA.

	Group.	Chitinous Structure.				Facets.			Pubescence.				Plates.[1]		Sexual Characters.				Ocelli.		
	Williston's Phyla.	Marked.	Lines Remaining.	Absent.	Double Eyes.	Circular.	Hexagons.	Two Sizes in ♂.	Much in ♂.	Less in ♀.	Equal ♂ ♀.	Absent.	Marked.	Simple.	Holoptic.	Dichoptic.	Equal.	Extreme Development.	Three.	Two.	Aborted.
Cecidomyidæ....	1	*				*						*						*		*[2]	*
Mycetophilidæ...	1	*				*					*		*			*			*	*	
Bibionidæ — *Bibio* ♂....	0		*		*		*	*	*					*	*				*		
Bibionidæ — *Bibio* ♀....	0			*			*					*		*	*				*		
Bibionidæ — *Dilophus* ♂.	0		*		*	*		*	*					*	*				*		
Bibionidæ — *Dilophus* ♀.	0		*			*				*				*	*				*		
Bibionidæ — *Scatopse* ♂ ♀	3	*				*					*	*	*			*			*		
Simulidæ.....	3	*					*	*				*	*			*					*
Chironomidæ....	2	*				*	*					*	*			*					*
Psychodidæ.....	1	*				*						*	*			*					*
Culicidæ — *Corethra* ..	2	*				*						*	*			*					*
Culicidæ — *Mochlonyx*	2		*			*						*	*			*					*
Culicidæ — *Culex*.....	2			*		*						*	*			*					*
Ptychoptera.....	1	*					*					*		*		*					*
Tipulidæ.....	1	*					*					*		*		*					*
Rhyphidæ.....	1		*				*				*			*		*			*		

[1] *Chironomus.*

[2] Exceptions exist.

To recapitulate, I think that group 1, with the inclusion of the Simulidæ, is a strong natural group, and even stronger tribe. Groups 3 and 4 fail altogether. Group 5 is fairly strong, but suggests the inclusion of the Stratiomyidæ, Xylophaginæ, Tabanidæ and Leptinæ, Lonchopteridæ and Phoridæ. As regards the Acanthomeridæ I have nothing to suggest.

TABLE VI.

STRUCTURE OF THE EYES IN BRACHYCERA AND CYCLORRHAPHA.

	Group.	Chitinous Structure.				Facets.			Pubescence.				Plates.		Sexual Characters.				Ocelli.		
	Williston's Phyla.	Marked.	Lines Remaining.	Absent.	Double Eyes.	Circular.	Hexagons.	Two Sizes in ♂.	Marked in ♂.	Less in ♀.	Equal ♂ ♀.	Absent.	Marked.	Simple.	Holoptic.	Dichoptic.	Equal.	Extreme Development.	Three.	Two.	Aborted.
Asilidæ	5	*					*	[1]			*	*		*		*			*		
Empidæ: *Clinocera*	5	*					*				*			*		*			*		
Empidæ: *Pachymera*	5		*				*					*		*		*			*		
Empidæ: *Hybos*	5			*			*					*		*			*	*	*		
Dolichopodidæ	5	*	*				[2]				*			*	*				*		
Phoridæ	4	*	*			*	[2]				*			*		*			*		
Lonchopteridæ	4	*					*				*	*		*		*			*		
Leptidæ	0	*					*	*			*	*		*	*				*		
Stratiomyidæ	3	*					*	*			*	*		*	*	*			*		
Tabanidæ: *Tabanus*	3	*					*	*	*					*	*				*		*
Tabanidæ: *Chrysops*	3		*				*			*		*		*	*				*		
Tabanidæ: *Hæmatopota*	3	*	♂	♂[3]			*	*	*	*				*	*						*
Tabanidæ: *Pangonia*	3	*					*	*				*		*	*				*		*
Bombylidæ	5	*					*				*	*		*	*				*		
Cyrtidæ	0										*	*		*					*		*
Oncodes	0	*					*					*		*		*	*		*	*	
Platypezidæ	4		*	*			*					*		*		[4]			*		
Pipunculidæ	4			*			*					*		*	*			*	*		
Syrphidæ	4	*					*	*			*	*		*	*				*		
Conopidæ	4			*			*					*		*	*				*		*
Muscidæ	4			*			*		*	*	*	*		*	*	*			*		

[1] In *Leptogaster cylindrica* Deg. (exceptional) ♀.

[2] Often squares.

[3] The three stages have been found in the eyes of *H. pluvialis* in ♂.

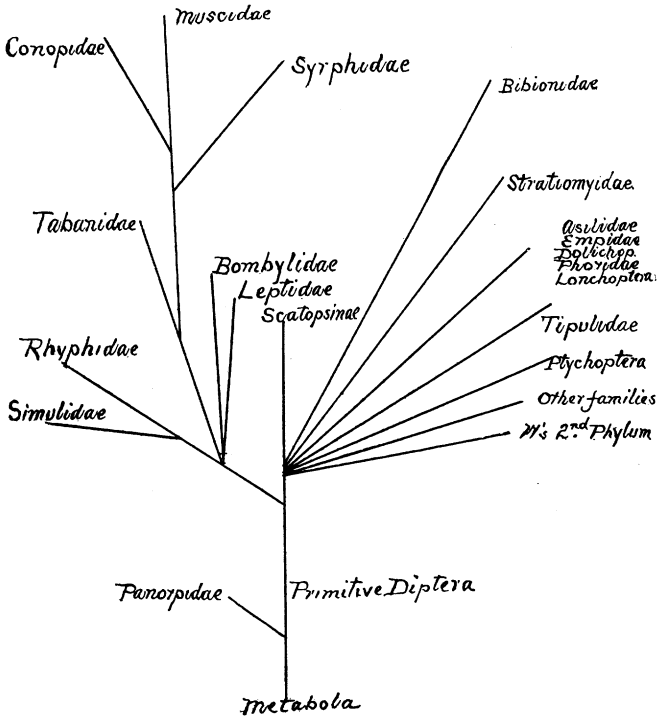
[4] *Opetia* exceptional.

With regard to the phylogeny of the Cyclorrhapha I have endeavored to show by a comparison of the mouthparts and venation, to which I may add the eye structure and general morphology, that the Tabanidæ stand close to the ancestral forms of the Cyclorrhapha, though the Syrphidæ and Conopidæ branched off when the insects had complete mouthparts and ocelli, long before the Muscidæ became the specialized and dominant group that it now is.

Williston says (page 332) that "every family save the Tipulidæ is, I believe, absolutely excluded from immediate genetic relations with the Brachycera, because of the venation and antennæ." I do not know of any anatomical structure that militates against

this view, and there are several that favor it; but I am strongly inclined to associate the Rhyphidæ with the Tipulidæ. The antennal characters and the venation are not insuperable objections; but I rely on the mouth, simple eyes and genitalia. The first of these characters is much less specialized than in *Tipula;* three ocelli are present, and the peculiar genitalia foreshadow those of the Tabanidæ and Leptidæ, while as I have already pointed out those of the Asilidæ, Stratiomyidæ and Dolichopodidæ and Empidæ seem to have been derived from a form like that of *Tipula.*

I venture to express these ideas in the shape of a tentative scheme, as follows:



If we are content to accept this view that the Rhyphidæ are close to the ancestral form of the Tabanidæ, we get another gleam of light on this obscure pedigree. If the idea is tested by the general morphology of the families it will be seen one section

is characterized by a comparatively large head, flat thorax and broad, flat abdomen; this includes the Rhyphidæ, Simulidæ, Tabanidæ and the Cyclorrhapha. The other section has a small head, humped thorax, and a narrow, depressed abdomen; this includes the Tipulidæ, and the Brachycera, except the Tabanidæ, Leptidæ, Therevidæ and Bombylidæ. The persistence of these two well-marked forms is good evidence of my argument, and, though it weakens the status of Williston's fifth phylum it establishes even more strongly his first and second.

On the Classification of the Nemocera.

If the table of the mouthparts of the older families is examined it will be seen that in only one family, the Cecidomyidæ, is the pharyngeal pump absent, but my specimens of this family are so few in number that probably this observation has no value. I feel confident that, with sufficient material, it will be demonstrated in some genera, even though vestigial. But, I am sure that *Bibio*, *Dilophus* and *Chironomus* do not have it, though it is present in *Scatopse* and some *Ceratopogones*. Not only are the Bibionidæ singular in this respect, but the eye structure, the limbs and bristle structure are all highly specialized. The usual coloration of certain species is singular and as remarkable as anything among Diptera, while the simpified venation and modified mouthparts mark them off as the most specialized family among the Nemocera. The only archaic characters remaining are the ocelli, the four-jointed palpi, and the long, membranous labium of *Dilophus*, with the palpi inserted near its end. In comparing the Chironomidæ with the Bibionidæ it will be seen that the mouth is less specialized, since the stipites and cardines are obvious and the mandibles are not fused, though embedded in the ventral side, as in *Bibio* and *Tipula;* the eyes are quite archaic in type, as is also the bristle and hair structure. Though the Culicinæ are highly specialized, the Corethrinæ are obviously older, and they possibly represent the continuance of an ancestral form of the Chironomidæ, as the venation is archaic and the mouth retains the pharyngeal pump.

These points show that the present arrangement of the families of the Nemocera, though convenient, is not founded on a true

principle. An arrangement which collocates those families possessing the most archaic characters would seem to be more proper. I would arrange Williston's groups 1 and 2 at the head of the Nemocera as follows:

1. Rhyphidæ.
2. Simulidæ.
3. Cecidomyidæ.
4. Mycetophilidæ.
5. Orphnephilidæ.
6. Psychodidæ.
7. Tipulidæ.
8. Dixidæ.
9. Culicidæ.
10. Blepharoceridæ.
11. Chironomidæ.
12. Bibionidæ.

I would place the Rhyphidæ first, since the venation is archaic, complete ocelli are present, the size is small and the pubescence and leg bristles are primitive. Add to these the structure of the mouthparts which appear to have their prototype in the Myriapoda, and it appears to me that the evidence is overwhelming that the family represents the most archaic type of Diptera; but I shall have more to say on this subject later.

The Simulidæ follow, as they also possess the peculiar structure of the palpi and have a nearly complete mouth-armature and are small in size. The Cecidomyidæ come next on account of the many-jointed antennæ and the archaic type of eye structure, but I admit that their place in the scheme is tentative. The Mycetophilidæ are difficult to separate from the Cecidomyidæ, but their eye structure, mouth, tibial bristles and the variable condition of the venation all justify their position here. The Orphnephilidæ are usually placed next to the Psychodidæ, which is a very old type retaining many archaic characters in eyes, mouth and wings.

The Tipulidæ follow as preserving the oldest type of venation, of leg pubescence and bristle-structure, together with the old types of eye structure, mouth and genitalia. The Dixidæ follow as the first family of Williston's second phylum. It is

difficult to say whether the Culicidæ or the Chironomidæ should have the precedence. The former are entitled to it on the venation (an obviously old form, possibly ancestral) and on the mouth, though I have a *Ceratopogon* in my cabinet with pharyngeal pump and broad-bladed maxillæ and mandibles, which is more primitive in type than the armature of *Culex*. But this is exceptional, the majority of the *Ceratopogones* being without mandibles and having the laciniæ of the maxillæ of a simpler type. The archaic type of eye structure is matched by *Corethra* and the absence of a pharyngeal pump in so many genera, whereas it is always present in the Culicidæ, decides in their favor.

The Blepharoceridæ follow, and the Chironomidæ after. I have already given my reasons for placing the Bibionidæ last.

Williston, in the true spirit of a paleontologist, has speculated on the primitive dipteron, and has given in words a reconstruction of a hypothetical form (p. 331, 2), as follows: "The primitive dipteron must have had eight fully developed longitudinal veins (including the auxiliary vein) with the second, third, fourth and fifth furcate, and a complete discal cell. The head was rather small, with the compound eyes separated equally by the front in both sexes. The ocelli were functional, and the maxillary palpi had four freely articulated joints; the labial palpi had probably already disappeared, though Weschè thinks differently. There were at least thirty-nine antennal joints in the male. The prothorax, mesothorax and metathorax were imperfectly fused, and the metanotum was visible from above. The abdomen had nine functional segments; the body was without differentiated bristles; and the tarsi had membranous pulvilli and empodia. The primitive flies were of moderate or small size, and probably crepuscular in habit, or at least denizens of shady forests."

Williston goes on to say that of modern Diptera the Tipulidæ approach most closely this hypothetical ancestor, principally in the venation, and remarks that they have become specialized by the almost complete loss of the ocelli, increase in size, and the loss of the pulvilli. He places the Rhyphidæ next in rank to the Tipulidæ. It seems to me, however, by his own diagnosis, that the Rhyphidæ are more primitive than the Tipulidæ. They

are small, and have functional ocelli and pulvilli. The mouth-parts are much less specialized (the mentum being developed) and they retain some remarkable archaic characters. I would protest against the time-honored custom of subjecting all other characters of Diptera to the venation.[1]

This reconstruction of the primitive dipteron by Williston has given me much pleasure and much food for thought, though I am not in agreement with him in his views of the labial palpi. I think that the primitive dipteron had, like all other contemporary insects, four palpi, and that they persisted in this condition until after the chief phyla had arisen, since a large majority of the Empidæ have what I believe to be undoubted labial palpi. I have no doubt that the structure of the labium in *Chrysops*, which I figured in 1904 in the cited paper on mouth-parts, shows aborted labial palpi, the palpigers. Savigny, in the dawn of orismology, pointed out remains on the labium of *Tabanus italicus*, and I can show a number of preparations in the same family with tufts of hair in similar situations to the palpigers of *Chrysops*.

Loss of Antennal Joints.

Williston discusses this subject on pages 328, 329 of the cited paper; some observations by myself may throw additional light upon it. I have in my cabinet a preparation of *Scatopse* of very small size, probably *S. minutissima* Verrall., in which the antennæ are unsymmetrical. The fourth and fifth joints are partially fused in the left antenna, the suture going only half through the segment; the right antenna has the full number nine of antennal joints, with the fourth and fifth separated (Figs. 1, 2); here we can clearly see that a middle joint has been lost. In preparations of *Dilophus* and *Bibio*, where, judging from the variations in number in different species, the antennæ are in an unstable condition I have several specimens where the distal joint consists of from three to six segments closely

[1] I will not quarrel with this conclusion, though I still think that holopticism outweighs in importance the archaic characters of ocelli and pulvilli and even of the mouth parts. It is quite evident, however, that the Rhyphidæ should no longer be placed at the extreme end of the Nemocera.—S. W. Williston.

joined together, the last or true terminal joint in an atrophied condition (Figs. 3, 4). It would thus seem that, in the antenna of *Dilophus* at least, joints may be lost either by fusion of the middle ones or the disappearance of distal ones.

The Character of the Hairs and Bristles on the Legs of Diptera and other Insects.

In the striking reconstruction of the primitive dipteron I have quoted, Williston has suggested that the body was without differentiated bristles. This character may well be extended to the limbs also. In 1902 I published some figures of the legs of diptera,[1] but these were mainly concerned with the strangest forms I could select; though the hairs and bristles were arranged in striking forms they were mostly subsidiary and depended on the altered shapes of the femora, tibiæ and tarsi. Later, in 1908,[2] I gave twelve figures of the microscopic appearance of preparations of legs taken from twelve different flies, three to illustrate a simple type, four the raptorial type, four the secondary sexual type, and one the parasitic type. The study of the limbs has led me to place considerable reliance on the hair and bristles as characters, and I find myself quite in agreement with Williston's idea that the simpler pubescence is the older form. My selection, a purely chance one, gave me as a result the legs of a tabanid, a leptid, and a stratiomyid as simple types. Going further back in an endeavor to realize what the primitive characters might be, I examined preparations of Myriopoda, *Blatta*, *Forficula* and *Panorpa*. These showed very wide differences in the bristles and hair with which they were more or less covered. Of the Myriopoda five species were examined, two Indian (Kashmir) and three British. A large *Scolopendra* is without pubescence, and with only two small bristles at the penultimate joint of the tarsi and two at the base of the claw. A species of *Scutigera* has an extraordinary number of tarsal joints (39) covered with short hairs, some of them short and stiff, with bristles at the larger joints, the parts that may represent the

[1] "Modifications of the Legs of Some Dipterous Insects." *Journal Queckett Club.*

[2] "On the Microscope as an Aid in the Study of Biology in Insects." *Journ. Royal Microscopic Society*, August, 1908.

coxæ, femora and tibiæ. Two British species (*Cryptops*) have short, stiff hairs regularly disposed over the legs; but a larger and broader species with a greater number of legs has them almost bare.

In *Blatta* a few short hairs are scattered over the limbs, but the femora and tibiæ are armed with many strong, sharp spines, which, in the genus *Phyllodromio*, are serrated with minute but regular barbs, undoubtedly specialized for raptorial purposes. In *Forficula* there are no bristles, only minute, soft scattered pubescence, which is much thicker on the inner side of the tarsi than elsewhere. In *Panorpa* a short, very even, uniformly long and regular pubescence is found studded with longer spines on the tibiæ and tarsi, and with tibial spurs of a curious and marked structure, each spur appearing as if it were made up of a number of fine hairs of various length, so that the edges appear almost plumose, certainly serrate.[1]

It may be of interest to record that *Peripatus novazealandiæ*, that remarkable survival, has neither pubescence nor bristles on its short forelegs or on any part of the skin, which, however, is studded with minute papillæ.

All these arthropods except *Peripatus* have one character in common, and that a very marked one. From the upper joints, or femora to the claw or claws, there is seen what under low magnification appears to be a thread-like tendon, but under high magnification a duct leading to the claw, either carrying poison to the claw or moistening the plate at the base of the empodium, and from that part the pulvilli. This duct might have been described from diptera instead of *Blatta*, *Forficula* or *Panorpa* so obvious are the homologies, but the arrangement of hair and bristles on the surface suggests no counterpart, except in *Panorpa*. A comparison of my preparations in the Nemocera with that

[1] In my paper on the systematic affinities of the Phoridæ in the *Transactions of the Entomological Society*, I stated that this structure was only to be found in the Mycetophilidæ and Phoridæ. I should have stated that only in the former family were they found in a size comparable and requiring a magnification of 250 diameters for elucidation. These on *Panorpa* and the diptera mentioned later are much larger and can be seen with lower powers, except in the case of the Rhyphidæ, which is a recent observation. Of course the presence of this structure in other insects admittedly of ancient type only strengthens my former argument, but it also shows the danger of dogmatic formulas.

insect shows that the pubescence of the legs approximated closely in *Gynoplistia bella*, particularly in the region of the tarsi; in *Ptychoptera albimana*, *P. lacustris*, *P. scutellaris*, and *Rhyphus fenestralis* the structure of the tibial bristles is practically identical. This is certainly remarkable, as Woodworth on the evidence of the venation[1] has suggested that this family is more closely related to the diptera than any other, branching off after the Neoptera had left the Metabola.

I think that we may assume that the primitive type of pubescence on the legs of diptera was somewhat similar to that which yet exists in *Rhyphus* and the Tipulidæ; and that when marked bristle structure or armature is found the insects are specialized. So we recognize, and this harmonizes well with other characters, that the Bibioninæ and the Culicinæ are the most specialized subfamilies among the Nemocera, such forms as *Dilophus*, or *Mucidus* and *Sabethes* making this clear. In the Mycetophilidæ, *Sciara* preserves the older type, while *Mycetophila* in the strong spines on the tibiæ and tarsi is more specialized, which idea is quite confirmed by the ocelli, three in *Sciara*, two in *Mycetophila*, and these remote from their usual position. The other families (I am not certain of the Blepharoceridæ) are all of the simpler types as is the genus *Scatopse* and the subfamily Corethrinæ.

Among the Brachycera, in the families with many genera, a number of variations between simplicity and complexity will be found, mostly as secondary sexual characters in the male, while the predaceous insects will be found modified in both sexes. The more striking examples of the latter will be found among the Empidæ, the Asilidæ appearing to confine their armature mostly to the tarsi. The Phoridæ have a peculiar and characteristic chætotaxy, but do not vary markedly; while the Leptidæ, Stratiomyidæ, Tabanidæ and Cyrtidæ are all of the simpler type, the Leptidæ most nearly like the Tipulidæ, retaining the peculiar bristle structure. The Platypezidæ and Pipunculidæ show various modifications of rows of long bristles or hairs as well as peculiarly modified bristles. In some Platypezidæ these bristles

[1] "Wingveins of Insects." Univ. California Publications, Entomology, Vol. 1, p. 145, 1906.

(as in *P. consobrina*) are, like the modified hind tarsi, found in both sexes.

Among the Cyclorrhapha, as might be expected, we find the characters of the legs extremely developed. Among the Syrphidæ, though there are many such simple forms as *Chilosia*, we find progressive degrees leading to great complexity, as in *Platycheirus* and *Pyrophœna*. Such a form as *Sphœrophoria scripta* is an intermediate one; the general type is simple, but the under side of the middle femora of the male is studded with short sharp hairs absent in the female. The four genera of the Conopidæ examined all show a greater specialization than *Sphœrophoria*. *Gastrophilus equi* has a long shaggy pubescence far removed from the simple forms. Of the Muscidæ alone a chapter might be written on the variations of the pubescence and bristles of the legs; and some flies, like *Glossina*, have structures which appear to be characteristic. All these modifications are those of strong bristles, though softer hairs are often present. I can not call to mind instances, unless it be *Calobata* where the pubescence is uniformly like that of *Gynoplistia* and the Panorpidæ, soft and weak.

On Certain Glands in the Mouths of Some Myriopoda and Diptera.

In the limb-like maxillæ of *Scutigera* (a centipede with compound eyes) there are organs of striking structure. In addition to the poison glands, which may easily be mistaken for tendons or overlooked, there are transparent chitinous bulbs communicating with apertures in the claws by ducts of moderate length. These bulbs are studded with a number of short tubular processes which show clearly when the edges of the organs are focused. These are peculiar structures of characteristic appearance, and are very unlikely to be confounded with other organs. I naturally reached the conclusion that these were poison glands, as the bite of the centipede, in addition to the punctures of the claws, is known to be poisonous. With this idea I was surprised to find in the maxillary palpi of *Rhyphus fenestralis* ♀ a similar structure which I have figured in the cited paper on mouth-parts, as sense organs. These communicate with the air by fairly large openings

in the walls of the palpi (Fig. 14). Unfortunately I have no preparation of the male of this species, but I find a similar structure in the male of *R. punctatus*, though smaller in size and with a shorter duct; as also in a Tasmanian species as well developed as in the former species. The differences between these two species in this respect are so marked that it is possible to separate them on this character alone (Fig. 13).

The uses of the organ are obscure, but they are probably similar in both the myriopod and the insects. The poison duct in the legs is quite similar to that part in the maxilla; it traverses many joints and opens underneath the claw between two bristles inserted at its base. Without a doubt it is the homologue of the duct which moistens the pulvilli in the flies. Again referring to the maxillary gland, my observations have not ended here, as the palpi of *Simulium reptans* ♀ and *S. ornatum* ♂ have similar structures, though they communicate with the air by a different opening. Moreover in the mouth of two British species of *Cryptops*, on the maxillæ, or more properly speaking the maxillipeds, and absolutely homologous in situation and structure, are similar glands to those found in the Indian *Scutigera*.[1]

That this structure should be found surviving in Diptera is exceedingly remarkable, but not more so than the fact that the duct which leads the poison to the many claws of *Scoliopendra* should be found in a precisely similar condition in nearly all insects. I have found it throughout Diptera, in *Blatta*, *Forficula*, *Panorpa*, Lepidoptera, Hemiptera, in fact in all insects where there are membranes on the claws that need irrigation.

I have studied the sense organs of insects for many years, and by comparing the large number of preparations, using modern optical methods and objectives I have become familiar with their appearance in the antennæ, palpi and mouths of Diptera, and many other insects. Unless I am greatly mistaken, and mistakes are easily made in such minute structures, I can say with confidence that there are found in the palpi of *Rhyphus* and *Simulium* homologous organs of peculiar structure; and judging from a comparison with *Scutigera*, this character is one of the

[1] I find the structure in a modified form in a small *Lithobius*, found in a garden in London.

most ancient hitherto observed in Diptera, a character which existed before there were winged insects, and consequently before venation, a character which is quite in agreement with the idea that the Rhyphidæ are among the most archaic types, the least specialized of all flies.

Summary of New Observations.

1. Ankylosis of middle joints of antennæ of *Scatopse*.

2. Fused distal joints in the antennæ of *Dilophus*.

3. Observations on the legs of myriapods and insects.

4. The tibial bristles of *Panorpa*, the Rhyphidæ, Mycetophilidæ, Tipulidæ, Leptidæ and Phoridæ are all of the same peculiar structure, and, excluding the Phoridæ, the general pubescence of the legs is approximately similar.

5. A peculiar structure exists in the mouths of some Myriapoda, and similar structures in the palpi of the Rhyphidæ and Simulidæ.

6. The pharyngeal pump has been found in the heads of the Rhyphidæ, Psychodidæ, a *Ceratopogon*, *Scatopse* and the Simulidæ; and it has been dissected out in a vestigial condition from the heads of *Hæmatopota pluvialis* and *Tabanus africanus* ♀.

7. A *Ceratopogon* with mandibles has been found.

8. An observation on the number of receptacula of *Lonchoptera flavicauda* is recorded.

9. A suggestion is offered that the peculiar genitalia of the Rhyphidæ have some affinity with those of the Tabanidæ and Leptidæ.

10. The mentum is fully developed in the Rhyphidæ, another important link connecting the Nemocera with the Brachycera.

Explanation of Plate.

Fig. 1. Di gram of left antenna of *Scatopse minutissima*, to show the partial ankylosis between fourth and fifth joints.

Fig. 2. Diagram of the right antenna of same insect, showing normal structure.

Fig. 3. Diagram of antenna of *Dilophus febrilis*, showing condition of distal joint.

Fig. 4. Diagram of antenna of *Dilophus albipennis* to show condition of distal joint.

Fig. 5. Gland (?) from the maxilla of *Scutigera*, highly magnified. Its situation is shown in Fig. 12*a*.

Fig. 6. Second tarsal joint of hindleg of *Gynoplistia bella* (Tipulidæ) to show pubescence under magnification of 60 diameters.

Fig. 7. Second tarsal joint of *Leptis scolopacea* under like magnification.

Fig. 8. Tibial bristle of hindleg of *Panorpa communis*. 60 diameters.

Fig. 9. Tibial bristle of hindleg of *L. scolopacea*.

Fig. 10. Tibial bristle of hindleg of *G. bella*.

Fig. 11. Second tarsal joint of hindleg of *Panorpa communis*, as seen with magnification of 60 diameters.

Fig. 12. Diagram of a segment from the mouth of *Scutigera* to show the maxillæ and situation of the poison (*b*) and other glands (*a*).

Fig. 13. Second joint of maxillary palpus of *Rhyphus punctatus*. Diagram in optical section to show gland (*a*) with duct opening in the anterior portion of the joint, and the sense organ which is probably olfactory (*b*), as seen with magnification of 300 diameters.

Fig. 14. Trophi of *Rhyphus fenestralis* showing the ventral side. The right palpus shows the sensory structure on its surface, while the left is drawn in optical section to show shape, situation and structure of the gland contained in interior, The mentum shows a distinct median structure, and below it are the submentum. and a portion of the pharyngeal pump. *m*, mentum; *sm*, submentum; *pp*, pharyngeal pump; *a*, gland; *l*, lacinia of maxilla. Drawn from several specimens mounted with and without pressure, showing structure under magnification of 300 diameters.

Fig. 15. Hypopharynx of *R. fenestralis* showing submentum, an unusual condition.

Fig. 16. Labrum of *R. fenestralis*.

Fig. 17. Second joint of palpus of *R. brevis* Walker, differing from *R. punctatus* in the size and attachment of the gland (*a*) and the character of the sense organ (*b*) and from *R. fenestralis* in the attachment of the gland to the wall of the segment, and in the character of the sense organ. Same magnification as Fig. 13.

Fig. 18. Tibial bristle of hindleg of *R. fenestralis*. Magnification of 300 diameters.

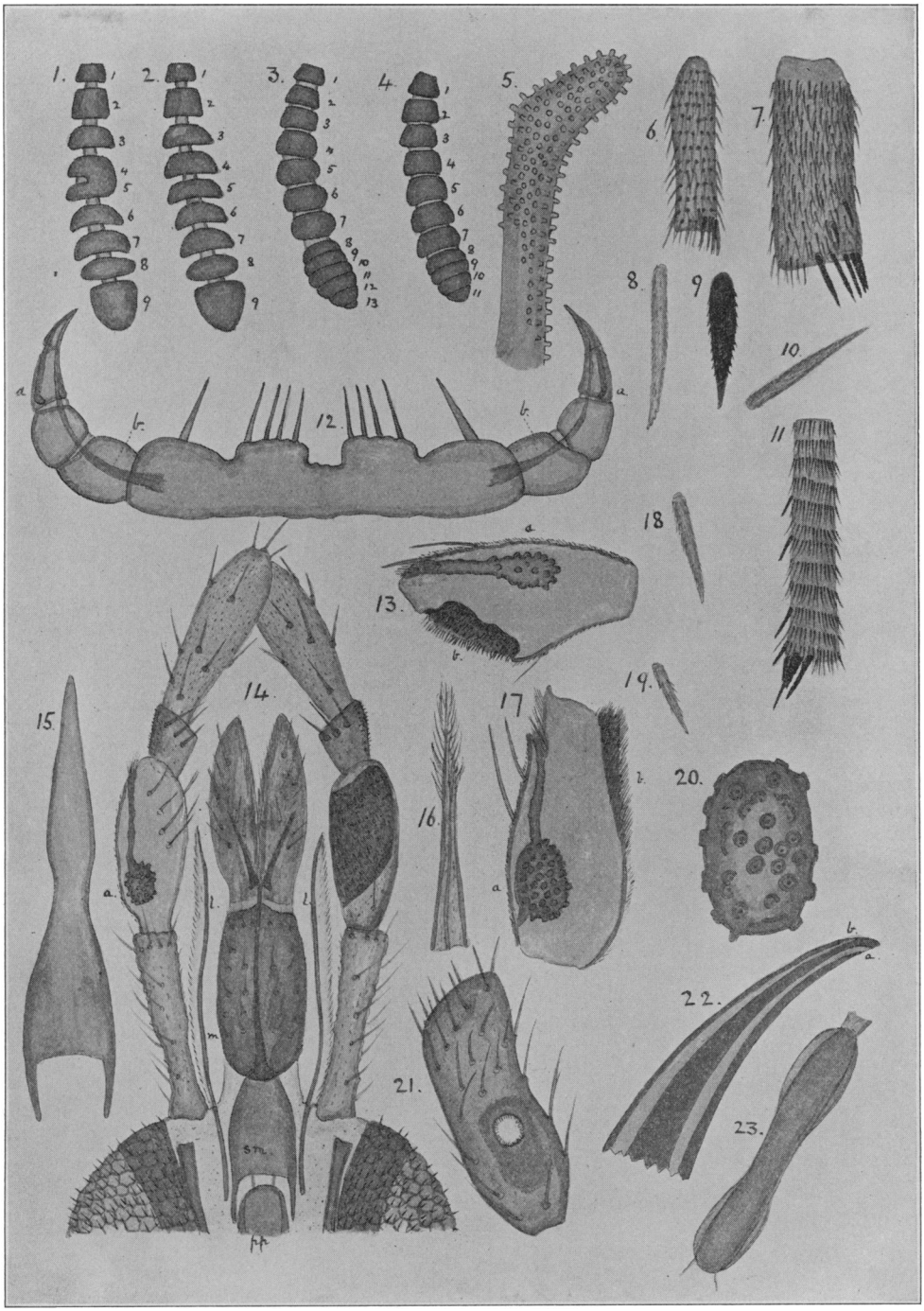
Fig. 19. Tibial bristle of hindleg of *R. punctatus*. Same magnification.

Fig. 20. Gland from interior of second joint of palpus of *Simulium reptans*, to show structure on side opposite the opening.

Fig. 21. Second joint of palpus of *S. reptans*, highly magnified.

Fig. 22. Point of maxilla of *Scutigera*, seen in optical section and highly magnified, showing openings of the poison duct (*a*) and of other gland (*b*).

N.B. The size of the figures has no relative significance.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